Report of Javier Rivas Salvador's PhD thesis: Habitat specialization as determinant of species response to the Global Change

General comment

The dissertation by Javier Rivas Salvador consists of four manuscripts. He is a leading author in two of them. The research is multidisciplinary and links community ecology, biogeography, invasion ecology, landscape ecology and evolutionary biology. The model species were birds. The PhD candidate studied the effect of habitat specialization on geographic distribution, conservation, interactions with alien species and population densities. I will not repeat the description of the content of these manuscripts given in the introductory section of the dissertation.

Two manuscripts have been already published in good journals and a further two have been submitted to ecological journals. Despite I liked these manuscripts I also have some reservations for statistical analyses and interpretation of some results. Due to the structure of the dissertation, I will give my critical points manuscript by manuscript. I hope that the criticism will be addressed by the PhD candidate during the defense.

Manuscript I.

This manuscript is very interesting. However, I have numerous statistical comments. My major concern is that the authors built separate models for geographical variables and climatic variables. I suppose it was done because geographic locations are strongly associated with climatic variables. However, building separate models precludes inference what is the major driver of species habitat specialization. Moreover, some modern statistical techniques would be perhaps able to separate the effects of climate from geography. I wonder if with such a large sample size (over 2000 cells) some other modelling framework might be more informative. For example, gradient boosted regression trees can easily be implemented using 'gbm' package in R (Ridgeway 2013). It would allow for the discovery of a nonlinear relationship between response and predictor variables (in a more elegant way than using the quadratic term - see Fig. S1 where the straight line is fitted to the nonlinear data), this method is also robust to the use of collinear predictors with complex interaction effects. Results of the gradient boosted regression trees can be depicted via partial dependency plots which are easily interpretable and account for the effects of other covariates. The 'gbm, calculates relative influence scores in very similar logic to the multimodel inference, but I believe they are free of shortcomings which importance calculated from the model weights have. Finally, the reporting of delta Akaike is unfortunate in table 1 a. Delta is usually defined (after Burnham and Anderson 2002) as the difference between the Akaike value for a given model and the best model (not reverse as authors did). In tables, the deltas Akaike are all below 0. The author stated that the best models were considered those with delta lower than 2. All reported deltas are lower than two. Sadly, this paper is already published.

Moreover, there are several issues listed below:

1. Lines: 184-185. Sentence: „All coefficients were lower than 0.7 indicating that multicollinearity did not apply to our models."

Why not use the variance inflation factor instead? At least some reference should be provided that this level of correlation does not affect statistical inference. Most of the published sources indicate that correlations only below 0.4 are acceptable in multivariate models.

2. Lines 148-149. Sentence: ".. analysis, we considered only the habitat categories covering at least 1% of the total area of a given cell."/

Did this removal impact results? Some very specialized species may occur in rare habitats. Rare habitats may have a disproportionally high impact on species richness thus perhaps should be included in analyses?

3. Lines 177-179. Sentence: „To assess the performance of each variable, we calculated its relative importance (Rel.Imp.) as a sum of Akaike weights of the models where a given variable was included."

Using variable importance was recently highly criticized (for example Galipaud et al. 2017, Methods in Ecology and Evolution, 8: 1668-1678).

4. In Table 2 models describing the effect of environmental variables on CSI_mean are odd. The model with a higher number of predictors has lower explained variance (R^2) than the model with a lower number of predictors. Usually, the inclusion of additional variables increases the explained variance. In my opinion, this may indicate that there indeed may be a problem with multicollinearity. This situation may happen when using R2-adjusted but this maybe was not the case as described in the footnote to the table. It seems that only one variable (longitude?) is driving the pattern in CSI.

I also noted several sentences and statements that were vague and which I could not agree with:

5. Lines: 76-78. Sentence: "…so that (ii) the mean and the variance in specialization will show opposite relationship to the environmental predictors."

This sentence is unclear. What author means by „opposite relationship to the environmental predictors". The predictions should be more specified.

6. Lines 331-333. Sentence: „...broad habitat niche was among the adaptations selected by orbitally forced range dynamics to survive the Quaternary climatic oscillations (Dynesius and Jansson, 2000)."

It is hard to agree with this statement. It suggests that the niche width is an adaptation, which is in my opinion wrong. Evolutionary forces act on individual traits. The niche width is a by-product of this selection.

7. Lines 346-351. Sentence: „In contrast, species found in temperate forest are mostly generalists breeding in a variety of woody habitats from forest interior to small woodlots, grassland-shrubland mosaics or even urban environment (e.g. Robin (*Erithacus rubecula*), Blackcap (*Sylvia atricapilla*) or Woodpigeon (*Columba palumbus*), Reif et al., 2016). We do not know, what are the supposed adaptations in these cases but we suggest that they may concern food requirements (such as bilberry for Capercaillie, see Storch, 1993)."

It would be useful to analyze which species traits differentiate between habitat specialists and generalists.

Manuscript II

The idea of this paper is exciting and important. I also liked the stated hypotheses. I think it would be nice to test this hypothesis for birds from the Annex II from the directive. However, my enthusiasm for this research is slightly diminished by a few problems that are not clearly described or addressed in the manuscript. My first concern is about using an index based on percentages. Why the author did not use the population size of a given species in a given country as a covariate in statistical models? I am very worried about this because it is easy to imagine that species population sizes of some species may be much lower in old member states of the UE than in new members and non-members. Thus it may be more straightforward to implement conservation measures to small population sizes confined to few areas (Western Europe) than to large populations spread over large areas (Eastern Europe). For example, it may be much easier to increase small population size e.g. from 10 pairs to 20, than from 1000 pairs to 2000 pairs (both increase by 100 %). These may be biologically very different phenomena when the population size increases from 10 to 20 pairs, and when it rises from 1000 to 2000. Let's take Corncrake (Crex crex) as an example. It is known that the largest populations of this species are in Eastern Europe and this species occurs only locally in Western Europe. Moreover, one can state that despite the decreasing trend the population size is high enough to sustain the species. I would say that a decreasing population of 1000 pairs of a species has better prospects for the future than the increasing population of 20 pairs of the same species. What I would like to see in the paper of this kind is showing the mean population sizes of studied species in three country categories. It is essential to understand if the studied index is not confounded with population sizes for each studied species (I would expect a negative correlation between the population size and the index). For example, I am curious to see if the average value of the correlation coefficient between the indices of population trend and population size among different country categories differ. But, as I said, the easiest way to cope with this problem would be including population size (e.g. starting population size) as a covariate for each species in each country.

My second concern is about the study design. I can hardly agree with the author's statement (lines 91-92) that "Such a design provides a strong test for the impact of listing the species under the Annex I." The division between old EU members, new EU members and non-members overlaps with the geographical gradient (old member states of the EU are located mostly in Western Europe). Thus, the estimated changes in the population sizes may result from other confounding factors such as climate variability.

My third concern is related to the presentation of results. I am confused by the presentation of the results in Table 3 and Figure 1. I am not quite sure what the coefficients for categorical variables in Table 3 mean. What was the reference category? I am confused because the effect of EU membership has three levels so I do not know, for example, what the

coefficient for „EU non-member states" equalling - 0.188 means. It is lower than -0.188 from what? I infer that these estimates are for the category of species „non listed in Annex I". Please, explain if I am right. Also, figure 1 does not help in resolving the problem because there is depicted only the effect of EU membership on species listed in Annex 1. What I would like to see is the same graph for species non-listed in Annex I. Such a graph would be the most informative. Last but not least, do not these estimates indicate an urgent need for conservation action of species not listed in Annex I?

Further issues:

1. Lines 272-275. Sentences: "By that means, the species recognized as deserving protection in EU are listed under the Annex I in all member states which results in protection of significant parts of their European (or even global) populations. This large-scale protection may then translate in population increase in all countries involved".

I think it is an idealistic vision rather than reality.

2. Lines 295-297. Sentence: „We found that the listed species had the most positive trends in the old member states and somewhat less positive in the new member states, but the difference between old and new member states was not significant."

Please, explain where I can find the statistical test for the difference in trend between country categories in Table 3?

3. Lines 315-319. Sentences: „However, a great contrast in the statistical effect of the species' listing between the new member states and non members indicates that this mechanism is hardly applicable. In addition, we did not observe any differences in mean bird population trends (after controlling the effect of listing) among old member states, new member states and non-members implying that presumably better environmental conditions in the Eastern Europe either recently deteriorated or did not mirror in positive bird population trends."

Don't these sentences contradict each other? If the difference in mean bird population trends is not different does it mean that listing to Annex I has a positive effect on overall species population trends? Also, I am very concerned that the statistical effect of differences in listing in Annex 1 on the bird population trend in EU members is driven only by the decrease in population trend in common species not listed in Annex 1. So the positive effect of listing in Annex I of the habitat directive in EU members is driven by the decrease in population size of non-listed species.

4. Lines 331-333. Sentence: „This is in clear contrast to our finding that the species listed as protected in EU have population trends more positive than the unprotected species".

Again, isn't that just the effect of decreasing abundance of common species but not the increase of population size of species listed in Annex 1.

Manuscript III

This manuscript is very interesting. The authors identified drivers of bird species richness in mid-field woods invaded by black locust and non-invaded woods. Conclusions are generally

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well supported by data. My major concern in this manuscript is that there is no comparison of bird communities found in mid-field woods with bird communities in the nearby arable fields. It remains unknown how invaded patches of woodland contribute to total/average species richness occurring in open fields. Of course, it seems clear that the contribution is lower than in the case of non-invaded mid-field woods. However, one may argue that even invaded woods may add several new species to these occurring in arable land. Also, I am very curious if invaded and non-invaded woodland patches change species composition and density of birds in the neighboring arable fields in the same way. I would also compare species composition in arable fields located far from any mid-field woodland patch. Such research would give a full picture of how mid-field woods affect birds in farmland. I would like to know the opinion of the PhD candidate on this; maybe he has some data on this topic.

I also noticed that authors mix different approaches to hypothesis testing in their manuscripts. They use both multi-model inference and traditional testing on P-values. Such an approach is often criticized as multi-model inference was proposed as an alternative to the usage of P-value. I think the authors could have used the Akaike Information Criterion and confidence intervals instead of reporting P-values.

Manuscript IV

Overall, this manuscript is an ecological study trying to link specialization level with population densities. The scientific problem is clearly formulated. However, some parts could have been prepared in more detail.

1. Lines 117-118. There is no mention of how the exclusion of rare species affected the results and how this could change their interpretation. Rare species are important in ecosystem functioning thus their omission seems odd (see: Jain et al. 2014. Ecol Evol. 4(1): 104–112.; Leitão et al. 2016. Proc. R. Soc. B.283: 20160084).

2. Lines 127-137. Paragraph "Response variables". Joining habitat variables is not explained satisfactorily. How joining these habitats could affect results? Some joins made me confused. For example joining "mountain" or "rocks" with "grassland" into one category: open habitat. First, mountains create specific conditions that enforce adaptations different than that found in open lowland habitats (Fjeldså et al. 2012. Annual Review of Ecology, Evolution, and Systematics Vol. 43:249-265). Thus, I am close to doubt if this join is biologically reasonable. Also, there is a poor description of how "geographical density" and "ecological densities" were calculated. I understand the idea of these two types of densities but some kind of equation would be very helpful to comprehend.

3. Lines 140-154. What was a correlation coefficient between ssPC and sfPC?

Lines 165-170. It is stated the Jetz et al. (2012) tree was used, but the Jetz tree is actually two different sets of trees, one based on constraints from Ericson et al. (2006; . Biology letters, 2(4), 543-547) and one based on constraints from Hackett et al. (2008; Science, 320(5884), 1763-1768). I am not sure which set was used but I hope authors used the Hackett tree set; this is what most users of the Jetz tree use. With all of that said, the Jetz tree is now showing its age. The analysis Jetz and colleagues used was constrained by the Ericson and Hackett "backbone" trees and by taxonomy. The use of taxonomy enabled Jetz et al. to include taxa for which there was no actual data, but led to some problematic results (see: Wang et al 2017, Journal of Biogeography, 44(1), 122-135). Moreover, there are parts of the Jetz topology for

taxa with no data that have 100% support. This probably reflects the difficulty of running the MCMC chain long enough to adequately sample the posterior distribution when so many taxa are included (Hosner et al. 2015; Journal of Biogeography, 42(10), 1883-1895). I am not opposed to including analyses using the Jetz tree because it is still the only really easy to use avian megaphylogeny, though it should be used with caution.

Final evaluation statement

In my opinion, the thesis by Javier Rivas Salvador is a valuable contribution to the science of ecology and conservation and undoubtedly meets the requirements laid down for the modern PhD theses. I recommend the thesis to be accepted by the scientific committee for the dissertation defence within the study programme Environmental Science at the Faculty of Science, Charles University.

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